HISTORY OF PLANT HYBRIDS.[1]

I. BEFORE 1761.

KNOWLEDGE of the existence of hybrids between various species of animals, especially between the horse and the ass, reaches back into the dim past. The conception of the possibility of hybridizing plants arose as soon as the sexuality of the higher plants became known. Toward the end of the seventeenth century it appears that simultaneously in several botanists the view took root that the stamens are the male organs of the flowering plants. In the year 1676 Grew brought before the Royal Society in London, in a paper which was published in 1682, Sir Thomas Millington's ideas concerning the sexual functions of anthers, which had not until then been made known.

The theory of the sexuality of the higher plants became more firmly grounded through Rudolf Jacob Cammerer (Camerarius) of Tübingen, who made his first experiments in 1691, and in 1694 published his *Epistola de Sexu Plantarum.* At that time he called attention to the possibility of the origin of plant hybrids, and later this question was often discussed by scientists but mainly only theoretically.

J. G. Gmelin saw several new larkspurs originate in his garden and decided upon their hybrid origin.

Linnaeus arrived at the opinion that the self-evident relationships of the species of plants could be explained

[1] Translated from the German by F. L. and E. H. Lewton.

by a common descent. He derived all the species which agreed in the construction of their flowers from the same mother stock, and all those plants resembling one another in form and shape of leaves from the same father stock. Following this same thought farther it appeared to him possible that the entire kingdom of plants was derived from a comparatively small number of originally created basic types. Holding this opinion, the study of newly-formed plant hybrids naturally had for him a special importance. One cannot state that he was especially fortunate in these investigations; upon superficial resemblance he declared as hybrids a number of plant forms which were of widely different parentage. Among those which were named spontaneous hybrids by him there are found only a few true hybrids. One of these is *Verbascum lychnitis* × *Thapsus*. But Linnaeus began to inaugurate experiments in artificial hybridization and with a little more patience would have arrived at important conclusions. He pollinated, for example, *Mirabilis longiflora* with pollen from *M. Jalapa,* an experiment which need only to have been reversed in order to have arrived at a remarkable hybrid. Linnaeus seems to have achieved good results in the crossing of *Tragopogon pratensis* and *T. porrifolius*. So far as I know no one has repeated the experiment, but the objections which have been brought forth by Koelreuter and others against the hybrid nature of the crosses described by Linnaeus can not be regarded as refutations because they refer to plants in the second generation. Linnaeus's *Tragopogon* is therefore, probably, the first plant hybrid originated for scientific purposes. It bloomed in 1759. Already much earlier, and even before 1719, an English gardener, Thomas Fairchild, had successfully crossed two pinks. The hybrid thus achieved, *Dianthus caryophyllus* × *D. barbatus,* was grown 100 years later in English gardens, and perhaps still is, as Fairchild's Sweet William.

This success in artificial fertilization was neither used for science nor does it seem to have given the gardeners an incentive to further investigations.

In spite of these isolated successful crosses the true history of plant hybridization does not begin before 1761; all that went before has more or less a traditional character, the few facts are buried beneath doctrinarian fantasies. As we have already said, Linnaeus made the attempt to gain firm ground in this realm, but it was Koelreuter who really founded the study of plant hybridization.

II. 1761—1799.

Joseph Gottlieb Koelreuter (born April 27, 1733, in Sulz on the Neckar; died at Karlsruhe, November 12, 1806) succeeded, after several unsuccessful attempts with other plants, in getting seed from a plant of *Nicotiana rustica* which he had fertilized with the pollen of *N. paniculata.* The hybrid plants derived from the above, bloomed in 1761. In this same year (1761) appeared the *Vorläufige Nachricht von einigen das Geschlecht der Pflanzen betreffenden Versuchen und Beobachtungen,* in which Koelreuter tells about his hybrid. In the same manuscript he told of a series of experiments whose full importance has only lately been recognized. He discovered the part played by insects in the fertilization of flowers; he determined the number of pollen grains which are needed for complete fertilization; and he gathered the nectar of flowers and showed that it was a solution of honey. In spite of the slight sympathy which he met with, Koelreuter continued his experiments and observations for several decades. All the essential characters of plant hybrids were correctly recognized by him. He fertilized, for example, a plant of *Nicotiana rustica* and its descendants regularly with pollen from *N. paniculata* through a period of generations (up to 20). In this way he transformed the first named species

into the second, and then with pollen of *N. rustica* brought it back again to the original mother form. He tried similar experiments with several species of *Dianthus*. He found out that the hybrid progeny of two species generally show an intermediate type and as a rule resemble each other exactly, it being immaterial which of the two types was used as the mother or father stock. The fertility of the crosses between several varieties of one species; the sterility or diminished fertility of hybrids between different species; the, as a rule, conspicuously greater growth of hybrids; and a mass of other remarkable facts were all carefully observed by Koelreuter. Although he knew of a number of cases of the spontaneous origin of garden hybrids, he never succeeded in finding natural plant hybrids. His successful crosses are principally between the species of the genera *Aquilegia, Matthiola, Dianthus, Melandryum, Linum, Malva, Lavatera, Lobelia, Nicotiana, Datura, Lycium, Verbascum, Digitalis,* and *Mirabilis*. But entirely apart from hybridization Koelreuter could through careful observation take glimpses into the household of Nature, the importance of which was not recognized till a hundred years later. Those important discoveries which were given in his first essay, have already been mentioned. Besides these he recognized the impossibility of the self-fertilization of many species of plants and the distribution by means of birds of plants bearing berries. He also made far-reaching investigations concerning the form of pollen grains.

Koelreuter's contemporaries gave his researches comparatively little attention, but science is indebted to the St. Petersburg Academy for the publication of his later works. With the exception of him and his brother Christoph Cunrad, hybrid plants seem only to have been raised by a few gardeners and flower lovers. For example *Papaver somniferum* × *P. orientale* in the Botanic Garden

at Edinburgh, also *Pelargoniums* by Wiegmann, Zeyher and others. It was not until 30 years later that Hedwig repeated the fundamental experiment of crossing *Nicotiana rustica* with *N. paniculata.*

Important observations concerning the morphology of the flower and provisions for fertilization in the Compositae were published by an Italian, Count Lavola, in the year 1764 in his *Discorso della irritabilita d'alcuni fiori nuovamente scoperta,* etc. Much later, in 1793, Conrad Sprengel's celebrated work appeared: *Das endekte Geheimness der Nature im Bau und in der Befruchtung der Blumen* ("The discovered secret of Nature in the construction and fertilization of flowers"). It is rich in interesting and exact observations concerning the relation between the form of the flower and insect visitors. These experiments appeared as a continuation and further development of Koelreuter's investigations which he had made public more than thirty years before. At that time they were given but little attention by scientists.

Toward the end of the eighteenth century another man appeared whose works concerning fertilization and hybridization have become of special importance, namely, Thomas Andrew Knight, the celebrated fruit and vegetable grower. Through the successful endeavors of the animal breeders, who tried to improve the domestic animals by crossing the different races, he came to ask the question if it were not possible by crossing races to obtain improved kinds of useful plants. Without knowing anything of Koelreuter he began his experiments with fruit trees and in 1787 with peas, by means of which he could get definite results much sooner. The progeny of his crosses between the races of peas made extraordinary gains in vigor and fertility. As early as 1799 Knight states "that nature intended that sexual intercourse should take place between neighboring plants of the species" (*Philos. Transactions,*

1799, Part II, page 202). He based this sentence upon his experiments with individual and race crosses, especially in the genus *Pisum*.

The important facts of fertilization had therefore been correctly recognized and made public at the end of the eighteenth century by several investigators. Koelreuter had discovered the importance of insects in the fertilization of plants; Conrad Sprengel had followed out in all their details the relationships between flowers and insects; Thomas A. Knight had demonstrated the advantages of crossing races. Although a few recognized the value of these facts this knowledge was not generally accepted and made a part of science. The real scientists followed the way opened to them by Linnaeus; they considered of most importance the recognition of species and their correct placing in genera and the higher systematic orders. But it is judging the spirit and endeavors of the time too superficially and too one-sidedly to believe that the species dogma crippled the free movement of thought.

The belief of the constancy of species was at that time not especially firmly grounded. Linnaeus himself, as we have before mentioned, was guilty of grave heresies against the doctrine of absolute and constant species. Medikus, the friend of Koelreuter, regarded as of no importance the question whether a genus comprised three different species or one species with three varieties. Duchesne, who introduced the conception of races into botany, was certainly far from believing in the constancy of species. Only the lack of a better understanding of known phenomena and facts prevented these and certainly many other men from taking a firm stand against the doctrine of the constancy of species. One would therefore be wrong in charging to doctrinal bigotry the fact that the discoveries of Koelreuter, Sprengel and Knight were so little regarded and understood. The truth is that these discoveries did not fit into

the idea of nature then current, for they could not be reconciled with then known facts and therefore were disregarded.

III. 1800—1825.

In 1800 there appeared J. E. Smith's *Flora Britannica,* a work in which for the first time two spontaneous hybrids between native species were introduced as parts of a European flora and expressed as *"β var. hybrida."*

To be sure, the hybrid *Verbascum thapsus* × *nigrum* was observed only in gardens and could therefore be classed with similar hybrids recorded by Linnaeus and Koelreuter. *Verbascum pulverulentum* × *nigrum* was, on the other hand, a true, spontaneous hybrid, originating in the wilds.

In 1809 there followed communications by Villars, concerning spontaneous hybrid *Gentians* (*Roem. Coll. Bot.,* p. 186), and in the following year a paper by J. D. Hoppe concerning a hybrid *Aconitum* (*Neues bot. Taschenbuch,* 1810, p. 217). The first clear and detailed description of the circumstances under which a wild-growing hybrid was observed, was given in 1823 by Guillemin and Dumas in their "Observations sur l'hybridité des plantes" (*Mém. Paris Soc, hist. nat.,* I, 79-92). As regards French achievements at this time in the realm of hybrids there may be mentioned the experiments of Sageret which were begun before 1820. From Bellardi there appeared in 1809 an article (*Saggio Botanico-Georgico*) in which were described several experiments on hybridization with cereals.

The disputes of the German scientists over the sexuality of plants and hybridization are noteworthy for their extraordinary fruitlessness. Schelver critically reviewed the theory of the sexuality of plants but did not find it sufficiently well grounded; which decision, however, was only possible because he cast aside Koelreuter's investigations and de-

ductions as unworthy of belief. Henschel further strengthened the belief in the non-sexuality of plants in that he tried to replace a total lack of uprightness and sense of truth by a skilful sophistry and by the overwhelming shamelessness of his assertions. The defense of the sexual theory was taken up mainly by L. Chr. Treviranus, who demonstrated in a strictly scientific way the facts in the case. But his laborious manner of writing could not compare with the unscrupulous arguments of Henschel, so that the latter, who was favored by those in power, seemed for a time to be the conqueror in this war of opinions. The quarrel partly turned on the truthfulness and trustworthiness of Koelreuter's assertions. Nothing would have been easier than that Treviranus, who believed in Koelreuter, should have repeated several of his experiments, which, after the way had once been shown, would certainly not have been too difficult for the superintendent of a botanical garden. Instead of that he allowed Henschel, who really made some experiments in hybridization, to surpass him even in this field. Henschel used these experiments for swindling instead of for earnest investigations. It would be an insult to the dignity of science to waste even a word over the assertions of Henschel. It is sufficient, as Godron has done, to mention Henschel's pretended hybrid between *Spinacia oleracea* and *Pinus strobus* to show the justness of this contempt. Finally, about the year 1819, the desire for reliable experiments in hybridization became more general.

While German science during the first quarter of the nineteenth century could show only unimportant or ignominious performances in the field of hybridization, English gardeners and flower-lovers, at the same time, made a great number of enlightening experiments. To be sure these were mainly in gardening but were also of scientific interest. Knight continued his crosses between different races or nearly related kinds of fruits and vegetables.

About 1808 R. J. Gowen, gardener of Lord Carnarvon of Highclare, and the English priest W. Herbert, began their long series of successful experiments in crossing plants, principally between species of *Erica, Rhododendron, Gladiolus* and *Hippeastrum.* A gardener, Thomas Milne, obtained the first hybrid in *Passiflora.* Robert Sweet busied himself with crossing species of *Pelargonium* and took great pains to establish the many varieties of *Pelargonium* raised by other plant-lovers and gardeners. Sweet's work, *Geraniaceae,* is perhaps the most comprehensive writing on hybridization which appeared during the first quarter of the nineteenth century. However, until now, not a single investigator in this field has paid any attention to it.

On the other hand, a sensation was aroused by the lively exchange of ideas between Knight and Herbert in the meetings and publications of the London Horticultural Society. Knight maintained that the hybrids between specifically distinct types were always sterile; fertile hybrids were always the result of crossing varieties. He said the fertility of a hybrid between two types, heretofore held to be different species, would, in spite of their dissimilarity, show that these were only varieties of a single species. (*Transactions Hort. Soc.,* London, IV, 367-373.) Herbert, on the other hand, had found that hybrids between manifestly different species are often fruitful; but he agreed with Knight in acknowledging that the possibility of producing a fertile hybrid or even a fertile cross between two plants, showed their original genetic relationship. He held that at one time there were only generic and family types which probably may not have exactly agreed with the present divisions of the botanical system. From these original types he derived the modern species not like Linnaeus, through hybridization, but like Lamarck and G. R. Treviranus, through "differentiation."[2]

[2] "I suspect that in the early periods of the world, there existed only the

The kernel of the whole dispute was the question of whether there existed a sharp and immovable boundary between fertility and infertility of the hybrids; but behind this question there was really a second, namely, whether there existed a sharp boundary between species and varieties. Species-hybrids should be sterile, variety-crosses fruitful. The Knight-Herbert discussion was a prologue to the later Cuvier-Geoffroy quarrel, which was played upon a much larger stage and with more comprehensive knowledge on the part of the actors.

IV. 1826—1850.

In England, the year 1825 continued to make additions to the history of hybrids. The gardeners continued to produce numerous hybrids and through Sweet, G. Don, Paxton, Lindley, Herbert and others, much has become known concerning the results of these crossings. The communications of Herbert, in an appendix to his work on the *Amaryllidaceae* and in a special essay in Vol. II of the *Journal of the Horticultural Society,* are most comprehensive. These papers were founded upon his own experience and that of others. His views are in general clear and reliable, even though not always complete enough for the strictly scientific investigator. At any rate, he has done more for the furtherance of our knowledge of hybrids than any other writer during the last half of the nineteenth century. In contrast to Koelreuter, Gaertner, and many later writers, he made his experiments almost entirely upon long-lived perennial plants.

During the period between 1825 and 1850 France can show especial achievements in hybridization. Several noteworthy papers we owe to Sageret and Lecoq, and several

distinct genera of plants, or heads of families, not however, exactly according to the present divisions of botanists." (*Trans. Hort. Soc.,* London, IV, 16.) Later, Herbert compared the origin of species from a common parent form with the development of the languages from a few original languages. (*Amaryllidaceæ,* p. 339.)

gardeners made observations upon accidental or intentionally made hybrids. In 1844 there appeared Godron's first work upon hybridity in the plant kingdom, with descriptions of some hybrids found growing wild.

More noteworthy are the German works during this period, although in reality they only sufficed to expose Henschel's deceptions and to substantiate to the highest extent Koelreuter's observations. By the agitation of Link, the Berlin Academy of Sciences in 1819 and again in 1822 offered a prize for an answer to the question: "Can hybrids be formed in the plant kingdom?" Finally there was sent in a paper by A. F. Wiegmann, to whom in 1826 half the prize was given. This work was published in 1828 under the title: *Ueber Bastarderzeugung im Pflanzenreiche.* The author agreed entirely with the views of Koelreuter and Conrad Sprengel. He made a number of unquestionable hybrids, besides some variations which he considered hybrids, the cause of whose origin has not even to-day been-determined. In the years following there were published several papers concerning successful crossing; for example, those of Christian Lehmann.

Of greater importance are the investigations of Carl Friedrich Gaertner (May 1, 1772 to Sept. 1, 1850). The first published work of this hybridizer was, to be sure, very presumptious. He had carefully studied the writings of Koelreuter and in the year 1825 made a great number of experiments in pollenization. He now wrote an essay on hybrid fertilization (*Naturw. Abh.,* Tübingen, I, 1), in which he pretended to be an experienced hybridizer and gave the results of his pollinations, most of which, as was later discovered, were only apparently successful. This essay was translated into French, and was undeservedly published in *Ann. sc. natur.,* X, 113-148. (1827). The tone of ripened experience which Gaertner adopted misled many to believe in his supposed results and in addition the sup-

posedly successful fertilizations were confused with the successful ones. This paper therefore became the source of great mistakes, though not entirely through the fault of the author. Later Gaertner was able to report an increasing number of actually obtained hybrids (published in *Flora*), and he continued his crossings through several decades. In number of experiments he has probably not been surpassed by any other hybridizer. His book: *Versuche und Beobachtungen über die Bastarderzeugung im Pflanzenreiche,* comprises the essential features of two of the author's papers which were submitted in competition for the prizes offered by the Kgl. Niederl. Akademie der Wissenschaften in 1830 and 1836,[3] together with communications offered in his scattered essays. It might be regarded as a working over of all the results obtained by his various experiments. Unfortunately, this very comprehensive work is extraordinarily dull; it is therefore on the one hand not well enough known and on the other its value is frequently overestimated. It is difficult to obtain a decided opinion upon the trustworthiness of the views expressed because the book contains numberless inaccuracies and contradictions. A careful, special study has convinced me that the mistakes in Gaertner's work were caused by an extraordinary lack of ability as a writer and his incapability to arrange in order his observations and facts. According to all appearances the author used his scattered notes concerning his observations about hybrids without ever reporting the deficiencies and incompleteness of the first investigations, even though later experiments showed entirely different results. Only thus can it be explained that the statements so often contradict each other. Among others, the remarks concerning the *Passiflora* hybrids on pages 241, 242, 288, 332 and 337 are characteristic. These

[3] The paper published in the Dutch language is little known and I have not yet seen it.

show how little Gaertner was able clearly to set forth a simple fact. Such sentences, in which the cause of the contradicting assertions can be seen, give the key to the understanding of the means of origin of many other wrong statements. The material which Gaertner worked over is confined almost exclusively within the lines laid down by Koelreuter.

Even though Gaertner's work is a well-filled revision of hybridization studies, one must never forget that it should be used with great caution and critical circumspection. More important and of greater service are Gaertner's investigations concerning the normal processes of fertilization.

Another branch of hybrid investigation reached conspicuous importance in Germany during the second quarter of the nineteenth century. Several able botanists had directed their attention about 1825 toward the hybrids found in a wild state. A. Braun, Wallroth, Zuccarini, G. W. F. Meyer, Ziz, W. D. J. Koch, and others, had recognized a number of spontaneous hybrids. Schiede, who had himself actively taken part in these investigations, collected all hitherto known facts on this subject. His little paper: "*De plantis hybridis sponte natis,*" appeared in 1825 and should be regarded as a forerunner in the study of hybrids in nature. Lasch and L. Reichenbach soon added new examples to the known cases of spontaneous hybrids, so that by 1832 A. P. de Candolle was able, in his *Physiol. végét.,* to complete Schiede's list. Especially valuable were later the careful investigations of C. Nägeli concerning hybrid *Cirsiums.* Fr. Wimmer, in connection with several friends (Krause, Wichura and Siegert), investigated with great success the hybrids in the Silesian flora. In spite of many mistakes in details correct knowledge concerning spontaneous hybrids made rapid progress. The conservative florists, to be sure, wished to know nothing of the many

hybrids, also many others, zealous for the doctrine of the constancy of species (for example Hornschuch), were against accepting so many because they were more inclined to believe in variations and intermediate forms.

V. 1851—1880.

The year 1850 marks a natural division in the history of hybrids. The death of the two most prominent hybridists in the first half of the century (Herbert in 1847 and Gaertner in 1850) on the one hand, the appearance of new investigators on the other, would have been sufficient to show a dividing line, even if there had not at the same time been developed a new tendency in the aims and endeavors of the investigators of hybrids. The first incentive to a lively discussion of the hybrid question came from J. F. Klotzsch. In a paper (*Verh. Kgl. Preuss. Akad.*, Berlin, 1854, pp. 535-562) he stated, among other assertions, that hybrid pollen is always sterile, that hybrids can never be fertilized with their own pollen, or with that of a third species, but only with the pollen of the parent form. In opposition to the experiences of Koelreuter, Gaertner, Herbert and numerous gardeners, this assertion was, in truth, more than bold. The first person who positively opposed this statement was E. Regel, who at that time had already had an extensive experience in the growing of hybrid *Gesneraceae*. Even though his crosses were made for gardening purposes, he did not lose sight of the scientific side of the question. Some of his most convincing proofs were taken from the genus *Begonia,* which Klotzsch had chosen for his especial study.

The usefulness of the discussion consisted principally in bringing to light a number of facts which otherwise would have remained entirely unknown. Moreover, for any unprejudiced person there could be no doubt in this case that Regel was entirely right.

Almost at the same time there developed in France another quarrel; namely, that concerning the *Aegilops* question. It was A. Godron who first destroyed the fanciful notions concerning the transformation of *Aegilops* into *Triticum,* through the origin of the artificial hybrid *Aegilops triticoides,* and who also proved by experiment that *Aegilops speltaeformis* came true to seed. A. Jordan's criticism of Godron's experiments, which is of value even at the present time, resulted in Godron and others (Grönland and Regel) endeavoring to establish the facts through repeated experiments in all directions.

The Klotzsch-Regel and Jordan-Godron discussions gave the incentive to further important investigations. On Jan. 30, 1860, the Paris Academy of Sciences decided to make use of a prize, which had been placed at its disposal, and to award it in the year 1862 for the best paper on "Hybridization in the Plant Kingdom." The Academy especially hoped to draw attention to three points, namely: the fertility or unfertility of hybrids; the cause of sterility, whether due to the pollen or the female organs; and finally the constancy of fertile hybrids through reproduction by seeds. Apparently the period of three summers which lay between the offering and the awarding of the prize, was much too short to begin and finish important new investigations. The Academy could only hope that the prize would be an incentive to a zealous continuation on the part of such men as had already busied themselves for some time with hybridization experiments, and to the publishing of the results of their endeavors. Two papers were handed in which were founded upon numerous experiments, the authors being Chas. Naudin and D. A. Godron. For sufficient reasons the Academy declared the work of Naudin to be the better and awarded him the prize, giving the work of Godron only honorable mention. The criticism of Duchartre on the decision of the Academy concerning God-

ron's work was not entirely without foundation. There is no doubt that in many respects Godron worked more carefully and thoroughly than his opponent. If one gives this scientific achievement a careful scrutiny it will be found surprising in one respect. In this prize paper Godron did not include all his former experiments, but considering everything the two experimenters described about thirty long series of experiments and noteworthy single experiments, to which must be added several incomplete observations and communications on facts long known. If one contrasts therewith the great mass of material which the investigations of Koelreuter, Herbert and Gaertner, not to speak of others, have furnished; then the material used by the two French investigators, though very useful, was apparently insufficient for a comprehensive and in some measure finished opinion on the subject.

Godron, as well as Naudin, founded his views concerning hybridization almost entirely upon his own investigations; the incomparably larger amount of his own and foreign experiences which Gaertner used in writing his work, was given practically no consideration. Moreover the two contestants had formed different ideas concerning the purpose of the prize. Naudin declared, clearly and decidedly, that in the meaning of Cuvier's theory there were no sharply defined species. "There is no qualitative difference between species, races and varieties; in searching for it one is pursuing a chimera. The three things are one, and the words by which one pretends to distinguish them, indicate only the degree of contrast between the comparative forms." (Cuvier, in *Ann. Sc. Nat. Bot.*, 4 ser., XIX, 201.) Naudin therefore saw no ground for considering nearly related but well characterized forms as anything else than distinct species. He found that there existed fertile and unfertile hybrids, but that the descendants of the fertile

hybrids more or less rapidly reverted to the parent type. Upon this last point Naudin placed the greatest weight.

Godron held fast to Cuvier's idea of species and was then still of the opinion that all hybrids between true species were entirely sterile[4] but were capable of being fertilized by the pollen of the parent forms or by that of another species. He held that through such recrossing there originated the richness of forms in the progeny of hybrids; that in general, the new forms would, in case they were protected from further crossing, be fixed and come true to seed. Fertile hybrids, in the first generation, isolated from their parent and related species, were not considered by Godron to be true hybrids between species, but were "blendings" whose parent forms were only races of one and the same species. Godron's entire view-point was governed by his experiments with the hybrids between *Aegilops* and *Triticum,* while Naudin was guided preferably by his observations on the *Solanaceae* and *Cucurbitaceae.* These two works are the sources from which numerous later botanical writers drew their views concerning plant hybrids; but no unprejudiced person will deny that in true worth they are conspicuously behind the works of Gaertner. The discouraging dullness and terrible confusion of the German investigator's presentation makes a study of this work, which is so rich in facts, very disagreeable; while the two Frenchmen developed their views in short, clear essays written in a fascinating manner. Their works, especially Naudin's, won in importance because the award by the French Academy stamped them as classics. The circumstance that the two authors contradicted each other in essential points should be regarded as fortunate for science, for otherwise their assertions would for a long time have been regarded as unassailable. Moreover, both Naudin and Godron continued their experiments so that their

[4] In his later articles Godron did not adhere to this mistaken opinion.

services to the science of hybridization are by no means to be found only in their competitive essays.

The next most important work concerning hybrid plants appeared in 1865. It was Max Wichura's *Die Bastardbefruchtung im Pflanzenreich, erläutert an den Bastarden der Weiden.* The numerous and painstaking experiments made by the author himself, are restricted to the genus *Salix,* in which he combined as many as six species into a single compound hybrid. In contrast to Godron, he confirmed the views of Koelreuter, Herbert, Gaertner, Naudin and others, that hybrids are frequently fertile to their own pollen, and also found, in contrast to Naudin, the progeny of hybrid willows to be constant. He thereby refuted the mistakes of his two nearest predecessors, whose works, moreover, he seems not to have known at all.

During the years 1865 and 1866 there appeared several noteworthy essays by C. Nägeli concerning the formation of hybrids in the plant kingdom. (*Sitzungsber. Akad. München, Math.-phys. Cl.*, 1865, II, 395; 1866, I, 71 ff., 190 ff.). Nägeli did not himself make any experiments in hybridization but he carefully observed numerous wild-growing hybrids. He was much more familiar with the literature of the subject than was Naudin, Godron or Wichura. For example, he deducted from the given facts in Gaertner's works the consequent conclusions. It was first through Nägeli that science was able to make use of the fruits won by Gaertner's experiments. To be sure Nägeli acquired some of Gaertner's tendency to doctrinarian views and the presentation of general theoretical dogma. Especially is this true in regard to Nägeli's theory of *Bastardirungsäquivalent,* in which he seeks to express numerically the degree of the resemblance of the hybrid descendants with the parent forms. He takes into consideration first, the part which each parent form takes in the production; second, the typical strength of these parent

forms, counting the number of generations needed to bring about the transformation. The fluctuation of characters, which is so common among the progeny of hybrids, as well as the tendency of reversion to the parent form, is sufficient to overthrow any such hypotheses and calculations. There is just as little support for the theory for the different influences of the male and female elements upon the characters of hybrids. Nägeli especially emphasizes the fact that it is immaterial for the systematic characters of the hybrids which of the parent species was the male or the female progenitor. The confidence which he put in Gaertner's statements would, by means of a sufficient number of his own experiments, have put him upon the right track. It is without doubt through Nägeli, that the theory of hybrids in the plant kingdom was for the first time completely demonstrated in an unprejudiced and connected manner. The scientific service of these works must be credited with great importance; they have been the source from which the text-books (like that of Sachs) and most of the later theoretical views concerning hybrid plants have been derived.

It is only necessary here to call briefly to mind the importance of Darwin's work on the doctrine of hybridization. To be sure Darwin's own experiments extended only in a few cases to crosses between species, but with great success he connected his investigations with Knight's experiences in the behavior of crosses between individuals and races. Moreover his experiments in the artificial fertilization of heterostyle species are extraordinarily useful.

Of recent scientific experiments in crossing Robert Caspary's hybridizations in the *Nymphaceae,* G. Mendel's with *Phaseolus* and *Hieracium,* D. A. Godron's with *Datura, Aegilops, Triticum* and *Papaver,* have to be regarded as especially instructive. Godron's series of experiments with *Datura* hybrids may be considered as the most prominent.

Through these experiments the fact was established, that from fertile hybrids having highly variable progeny, there can be produced, in the course of a few generations, races having mixed characters and coming true to seed. For new actual experiments with the characters of hybrids we have to thank Godron more than any other investigator of the nineteenth century.

The numerous crosses which were carried out by Gaertner during the last ten years have advanced the scientific knowledge of hybrids comparatively little. But of great interest are the hybrids of *Sarracenia, Nepenthes,* and numerous orchids produced by the English breeders, Seden, Dominy and others. Kellermann has communicated good observations concerning the hybrid *Araceae* raised by him.

Since 1830 the study of wild-growing hybrids has made important progress. To be sure the unprofessional have worked in the field as zealously as the professional; a careful examination of their views is therefore urgently requested; also because most of the florists have known little more to tell than the recognizable characters of the hybrids observed by them. The most numerous and important communications concerning wild-growing hybrids have been offered by Fr. Schultz, Timbal-Lagrave, Grenier, A. Kerner, Wirtgen, Michalet, Ritschl, Beckhaus, P. Ascherson, R. von Uechtritz, J. Schmalhausen, C. Haussknecht and V. von Borbás, not to mention numerous local florists.[5]

Through Fr. Schultz the investigations were often led into false paths, in that this erudite botanist held, with a certain fanaticism, the view that each hybrid combination appeared in two forms, according to which one of the parent species had yielded the pollen. He regarded it to be his duty, when finding a hybrid, to recognize from its characters which of the parent species had been the seed parent and which had yielded the pollen. His example

[5] Nägeli, Godron, Wimmer and others have already been named.

misled others to similar mistakes. Only gradually has this trifling been given up. On the other hand there has recently come to the front a tendency to use hybrids as material for the manufacture of new names. Nevertheless our knowledge of spontaneous hybrids has been considerably widened through the observations of the florists. One of the newest pertinent treatises; namely, that of J. Schmalhausen (*Bot. Zeit.*, 1875, pp. 520, 534), indicates how in the future the study of spontaneous hybrids may be of real use to science.

There was published by K. A. Kenniger in 1879 in the 62d volume of *Flora,* a compilation of the spontaneous hybrids found up to that time in Germany and Austria; remarks upon these by Otto Kuntze are to be found in Vol. LXIII, No. 19.

If one bears in mind the knowledge concerning hybrids in its principle features, he can take from it a decided lesson: *No greater mistake can be made than to try to generalize from a few single experiments.* Without doubt one can lay down well founded rules concerning the general behavior of hybrids, but one must not forget that for each of these rules more or less numerous exceptions will be found. In contrast to the unbending laws which rule inanimate nature, organisms show a certain freedom in their life phenomena, an unrestrained flexibility. Physiology must keep this fact in mind if it wishes to know and investigate with an unclouded view the transformations of which the plant form is capable under the influence of inner and outer forces.

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